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Response of microbial community composition and activity in agricultural and grassland soils after a simulated rainfall

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Abstract

Rainfall in Mediterranean climates may affect soil microbial processes and communities differently in agricultural vs. grassland soils. We explored the hypothesis that land use intensification decreases the resistance of microbial community composition and activity to perturbation. Soil carbon (C) and nitrogen (N) dynamics and microbial responses to a simulated Spring rainfall were measured in grassland and agricultural ecosystems. The California ecosystems consisted of two paired sets: annual vegetable crops and annual grassland in Salinas Valley, and perennial grass agriculture and native perennial grassland in Carmel Valley. Soil types of the respective ecosystem pairs were derived from granitic parent material and had sandy loam textures. Intact cores (30 cm deep) were collected in March 1999. After equilibration, dry soil cores (approx. −1 to −2 MPa) were exposed to a simulated Spring rainfall of 2.4 cm, and then were measured at 0, 6, 24, and 120 h after rewetting. Microbial biomass C (MBC) and inorganic N did not respond to rewetting. N_2O and CO_2 efflux and respiration increased after rewetting in all soils, with larger responses in the grassland than in the agricultural soils. Phospholipid fatty acid (PLFA) profiles indicated that changes in microbial community composition after rewetting were most pronounced in intensive vegetable production, followed by the relict perennial grassland. Changes in specific PLFA markers were not consistent across all sites. There were more similarities among microbial groups associated with PLFA markers in agricultural ecosystems than grassland ecosystems. Differences in responses of microbial communities may be related to the different plant species composition of the grasslands. Agricultural intensification appeared to decrease microbial diversity, as estimated from numbers of individual PLFA identified for each ecosystem, and reduce resistance to change in microbial community composition after rewetting. In the agricultural systems, reductions in both the measures of microbial diversity and the resistance of the microbial community composition to change after a perturbation were associated with lower ecosystem function, i.e. lower microbial responses to increased moisture availability.
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1. Introduction

Agricultural and grassland ecosystems have contrasting land use histories that may greatly affect soil quality. Agricultural tillage practices disrupt stable aggregates and decrease soil C within soil aggregates (Six et al., 1998). Soils under long-term cultivation show significant reductions between 30–50% of native soil C content (Lal, 2002), resulting in decreases in associated labile C pools and microbial activity, such as respiration. Grassland soils typically have greater soil organic matter (SOM) content and labile C pools. Thus, they have higher potential to immobilize and retain N (Barrett and Burke, 2000), resulting in greater potential N availability. In addition, agricultural and grassland soils support distinct microbial communities that are correlated with factors that define soil quality, suggesting that land use history and the associated soil quality influence microbial community composition (Calderón et al., 2000; Steenwerth et al., 2003).

As land use intensification increases and soil quality is degraded, it has been hypothesized that the diversity of soil

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organisms will decrease (Swift et al., 1996), and the resistance and resilience of a community to disturbance both decrease because fewer organisms exist that can adapt to the disturbance. In agricultural soils, the microbial community has typically been exposed to long-term and frequent soil disturbance in comparison to grassland soils. Agricultural soils therefore may have lower diversity, different composition of soil microbial assemblages, and less resistance to changes in composition and activity than grassland soils when exposed to a short-term perturbation.

Wet–dry cycles are short-term perturbations that can increase the availability of both C and N substrates in soils (Kieft et al., 1987) as well as elicit dynamic responses from soil microbes in terms of N mineralization, nitrification, denitrification, efflux of trace C and N gases from the soil, and community composition (Davidson et al., 1992; Lundquist et al., 1999a,b; Panek et al., 2000). Microbial biomass, respiration, and soil concentrations of dissolved organic carbon (DOC) also can increase rapidly after rewetting dry soil (Lundquist et al., 1999a). In addition, rewetting can result in microbial stress because it causes rapid changes in microbial osmotic potential, resulting in cell lysis (van Gestel et al., 1992).

To examine the relationship between land use intensification, soil microbial communities, and their activity, a short-term perturbation of soil rewetting was applied to two pairs of grassland and agricultural ecosystems on similar soil types in the Central Coast region of California. Distinctly different soil microbial communities were known to be associated with each type of land use (Steenwerth et al., 2003). The responses of C and N dynamics and microbial community composition to the short-term perturbation were measured to determine (1) if alterations in soil microbial community composition may be concomitant with changes in C and N dynamics after rewetting, (2) if there were divergent responses in soil microbial communities among grassland and agricultural ecosystems, and (3) if intensive agricultural management resulted in less resistance to change in microbial community composition and activity.

2. Materials and methods

2.1. Sites, vegetation and crops

In March 1999, intact soil cores were taken from perennial and annual grassland ecosystems and agricultural fields representative of typical land uses in California's Central Coast region. Four sites were chosen from a survey of 42 sites with different land use history and land use intensification in Carmel and Salinas Valleys, Monterey County, CA, USA in relation to soil characteristics, management (e.g. application of fertilizer, irrigation, herbicide, tillage, grazing), and microbial community composition (Steenwerth et al., 2003). They were selected because their microbial communities were representative of those associated with the specific grassland and agricultural ecosystems on the same soil types in the region. Two pairs of grassland and tilled, agricultural fields were chosen that shared sandy loam soil textures and all were derived from granite parent material (Table 1). The pair in Salinas Valley was composed of ecosystems dominated by annual plant species, whereas the pair in Carmel Valley consisted of ecosystems dominated by perennial plant species. The two sets of sites were 25 km apart.

Table 1
Soil characteristics of ecosystems in Salinas and Carmel Valleys

	Salinas Valley		Carmel Valley	
	Salinas Vegetable	Salinas AnnGrass	Carmel AgPerGrass	Carmel PerGrass
Sand (%)	72	69.5	62.5	62.5
Silt (%)	20	23.5	28	22
Clay (%)	8	7.0	9.5	15.5
Bulk Density ($g\ cm^{-3}$)	1.44	1.40	1.15	1.06
Exchangeable-Ca (meq $100\ cm^{-3}$)	15.0	11.5	9.3	5.5
Exchangeable-Mg (meq $100\ cm^{-3}$)	2.8	1.6	3.0	1.4
Exchangeable-K (meq $100\ cm^{-3}$)	1.1	1.0	0.7	0.5
pH	7.5	6.3	6.5	5.6
% C ($g\ cm^{-3}$)	1.26	3.77	1.24	2.41
% N ($g\ cm^{-3}$)	0.14	0.36	0.12	0.20
Total PLFA ($\mu g\ g^{-1}$)	11.7	33.8	12.9	39.1

This is a subset of data from Steenwerth et al., 2003.

The Salinas Valley sites were on Chualar sandy loam soil (Fine-loamy, mixed, thermic Fluventic Haploxeroll) and consisted of irrigated vegetable production vs. cattle-grazed annual grassland. The conventional vegetable field ('Salinas Vegetable') had supported two lettuce or cole crops per year for more than 50 y, experienced year-round cultivation, irrigation for several months per year, fertilizers ($\sim$100–300 kg N ha^{-1}), and frequent herbicide and pesticide applications. When intact soil cores were removed, lettuce seedlings were present in the vegetable field in the annual ecosystem pair. Prior to planting the lettuce seedlings, it had been fallow since the previous Fall. The annual grassland ('Salinas AnnGrass') supported exotic European annual grasses that senesce after setting seed in spring. They were grazed yearly under a seasonal rotation regime.

In the Carmel Valley, the paired grassland and agricultural sites were on Gorgonio sandy loam soils (Sandy, mixed, thermic Fluventic Haploxeroll). The land uses were perennial grass agriculture ('Carmel AgPerGrass') and native perennial grassland ('Carmel PerGrass'). In 'Carmel AgPerGrass', purple needlegrass (*Nassella pulchra* (A. hitchc.) Barkworth) was grown for seed production, and was irrigated intermittently during

peak plant growth periods. Three years prior to core extraction, it had been planted in perennial bunchgrasses, and had been cultivated for grain crops for several decades beforehand. 'Carmel PerGrass' supported relict perennial bunchgrasses, native annual and perennial forbs, and non-native annual grasses. Soil cores were only removed from areas directly under *N. pulchra.* Grass species at 'Carmel AgPerGrass', 'Carmel PerGrass', and 'Salinas AnnGrass' were in the reproductive phase of Spring growth when the cores were removed.

2.2. Climate

The region has a Mediterranean climate. Rain typically falls during the late Fall through early Spring followed by a summer drought. Precipitation from Fall 1998 to Spring 1999 (i.e. September–March) preceding soil core collection was 320 mm in Salinas Valley and Carmel Valley, while the average precipitation for the region is 520 mm (Cook, 1978). Spring is warm (mean daily maxima between 16.3 and 22.2 °C during March–May) with intermittent rainfall.

2.3. Soil sampling

Over 2 weeks in March 1999, 16 cores were collected from each site by driving PVC pipes (30 cm deep × 15.4 cm dia.) to a 30 cm depth in the ground. After removal, the soil cylinders were immediately transported to UC Davis and stored in a greenhouse with controlled temperature (mean daily maxima of 22 °C). Immediately after arrival at the greenhouse, aboveground plant material was clipped and any litter was removed from the surface of the cores.

Soil moisture retention curves were determined using a pressure plate apparatus. During the soil equilibration period, soil moisture within the cores was maintained between −0.55 and −0.70 MPa by watering two to three times per week, as monitored with tensiometers (Soil Moisture, Inc., Santa Barbara, CA) until the experiment began in July 1999.

At the beginning of July 1999, the bases of the soil cores were sealed with an acrylic plastic impermeable to O_2 and watering was ceased, causing the 0–12 cm layer to dry to approximately −1.0 to −2.0 MPa. Cores were then equilibrated to temperature and relative humidity in a growth chamber for 7 d before the initiation of simulated rainfall. The growth chamber was maintained at 25 °C, 70% relative humidity, and ambient CO_2 (350–370 $\mu l\, l^{-1}$) to simulate Spring conditions in the Central Coast region. Cores were re-wetted slowly with 445 ml distilled water over a 6 h period to simulate 2.4 cm rainfall, which is equivalent to a single large rainfall in the region.

After gas measurements were collected, soils cores were destructively sampled from 0–6 cm at 0, 6, 24 and 120 h after rewetting started. Microbial biomass C (MBC) was determined by fumigation extraction (Brookes et al., 1985; Vance et al., 1987). Organic C in the K_2SO_4 extracts was measured by analyzing diluted extracts (1:10) on a Phoenix 8000 automatic analyzer (Dohrmann [Tekmar-Dohrmann], Manson, OH) according to the method of Wu et al. (1990). Soil microbial biomass C was calculated from the relationship: biomass C = E_C/k_{EC} (E_C = [organic C extracted from fumigated soil] − [organic C extracted from non-fumigated soil]; k_{EC} = 0.45) (Wu et al., 1990; Joergensen, 1996). Soil respiration was measured by placing soil in sealed bottles and measuring the headspace CO_2-C concentration after 60 min. Inorganic N was extracted with 2 M KCl. Nitrate (NO_3^- − N) and ammonium (NH_4^+ − N) were analyzed with a Lachat Quick Chem II Flow Injection Analyzer (Zellwegger Analytical, Milwaukee, WI). Gravimetric moisture was determined after drying soil at 105 °C for at least 48 h. Potential net N mineralization was measured during anaerobic incubation (Waring and Bremner, 1964). Effluxes of N_2O-N, NO-N, and CO_2-C were measured in situ on capped cores (Folorunso and Rolston, 1984). Samples for N_2O were analyzed on a HP 6890 gas chromatograph with an ECD detector. CO_2-C efflux was analyzed with a gas chromatograph (HP 5890A with TCD). NO-N flux was measured immediately by chemiluminescence (Sievers Instruments Model 270B Nitric Oxide Analyzer, Boulder, CO). NO-N was not measured before rewetting as it was assumed to be negligible due to low soil moisture content (Meixner et al., 1997).

Bulk density and gravimetric soil moisture were measured in each soil core during destructive sampling. Soils were then air-dried, large roots (>1 mm) were removed with tweezers, and soils were sieved (<2 mm). Rocks >2 mm were weighed. Sieved soils from each site were analyzed for pH by saturated paste (US Salinity Laboratory, 1954) and particle size distribution (Gee and Bauder, 1979). Total soil C and N were determined by combustion (Pella, 1990). Texture, pH, and % total C and N were measured by the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California, Davis.

A separate set of samples was simultaneously obtained from each core for PLFA analysis from the 0–6 cm depth of each soil core. This soil was stored at −20 °C until extraction. Immediately before PLFA analysis, soil from each frozen sample was mixed, and all visible root fragments were removed with tweezers. Three subsamples were analyzed per core sample. A sample was also taken for gravimetric moisture by drying soil at 105 °C for 48 h. Soil samples (7 g dry wt.) were extracted using a modified Bligh and Dyer (1959) method as described in Bossio and Scow (1995). Total extractable PLFA provides a measure of microbial biomass at each site (Zelles et al., 1995). Assuming that as the number of species increases, the number of different PLFA also increases, the number of detected PLFA before rewetting was used as an estimation of microbial diversity before perturbation of the

Table 2
Summary of plant species found within an ecosystem in Carmel and Salinas Valleys

Salinas Valley		Carmel Valley	
Salinas Vegetable	Salinas AnnGrass	Carmel AgPerGrass	Carmel PerGrass
Lactuca sativa seedlings	*Brassica nigra* *Bromus rigidus* *Bromus hordeaceous* *Erodium circutarium* *Hordeum* spp. *Medicago hispida* *Vicia* spp.	*Hypochaeris* spp. *Nassella pulchra* *Poa annua*	*Anagallis arvensis* *Avena barbata* *Bromus rigidus* *Clarkia* spp. *Erodium circutarium* *Festuca* spp. *Gallium* spp. *Hypochaeris* spp. *Medicago hispida* *Nassella pulchra* *Poa annua* *Plagiobothrys collinus var. fulvescens* *Taeniatherum caput-medusae* *Vulpia microstachys*

microbial community by rewetting. Changes in ratios of 17 cy:precursor (16:1ω7c) and the sum of monounsaturated PLFA to saturated PLFA were used to detect changes in physiological status of the soil microbial community (Guckert et al., 1986; Kieft et al., 1994, 1997).

2.4. Vegetation sampling

During removal of the soil cores, three 0.25 m[b] plots within 1 m of randomly selected soil cores were clipped for plant biomass and later sorted by species and dried at 60 °C. Plant species richness (i.e. number of total species), diversity (i.e. Shannon diversity index), and evenness (i.e. uniformity in distribution) were calculated to characterize the plant community composition of the four sites (Kent and Coker, 1992). Plant species nomenclature follows Hickman (1993).

2.5. Statistical analysis

Differences in soil moisture, plant community composition, C and N dynamics, and specific PLFA based on valley (i.e. Carmel vs. Salinas), ecosystem type (i.e. agriculture vs. grassland), and time after rewetting were determined using a nested General Linear Model (GLM). The model for valley and ecosystem type used to analyze the differences in plant community composition included the main effect of valley and ecosystem type nested within valley. The model for valley, ecosystem type, and time after rewetting included the main effects of valley and time, and ecosystem type nested within valley. Valley*time and ecosystem (Valley)*time were the interaction terms. Differences between samples were based on GLM results and post-hoc Tukey's test ($\alpha = 0.05$). All univariate statistics were obtained using SAS version 8.2 (SAS Institute, Cary, NC, USA). Respiration, CO_2-C efflux, NO-N, N_2O-N, MBC, NH_4-N, and 17cy:pre were transformed by $\ln(x+1)$ to normalize the data for analysis. All data for these variables were reported and discussed as transformed values.

Canonical Correlation Analysis (CCA) of CANOCO version 3.11.5 (CANOCO, Microcomputer Power, Ithaca, NY, USA) was used to compare PLFA profiles between and within sites. The CCA analysis utilized the 22 PLFA in common between all sites and all sampling times. In each valley pair, tests of the CCA analyses indicated strong differences between the agriculture and grassland sites according to ecosystem type. Rather than present the results for each pair of sites, four CCAs are shown that were constrained for time since rewetting (e.g. 0, 6, 24 and 120 h) for an individual site (e.g. 'Carmel AgPerGrass', 'Carmel PerGrass', 'Salinas AnnGrass' and 'Salinas Vegetable').

3. Results

3.1. Vegetation analysis

Plant species biomass and composition differed within each pair of grassland and cultivated ecosystems (Tables 2 and 3). The Salinas Valley sites had greater

Table 3
Means and standard errors ($n = 3$) of vegetation characteristics of ecosystems in Carmel and Salinas Valleys

	Salinas Valley				Carmel Valley			
	Salinas Vegetable		Salinas AnnGrass		Carmel AgPerGrass		Carmel PerGrass	
	x	±SE	x	±SE	x	±SE	x	±SE
Biomass (g m^{-2})	1.67*[a]	0.04	653.7	38.7	31.0*	14.3	177.0	31.3
No. of plant species	1.00*	0.00	5.75	0.75	2.00*	0.58	11.25	0.75
Shannon Index[b]	0.000*	0.000	1.015	0.067	0.220*	0.110	1.573	0.078
Evenness Index[b]	0.000*	0.000	0.199	0.012	0.117*	0.065	0.417	0.42

* indicate significant differences between ecosystem types in each valley.
[a] $P < 0.05$*
[b] Kent and Coker (1992).

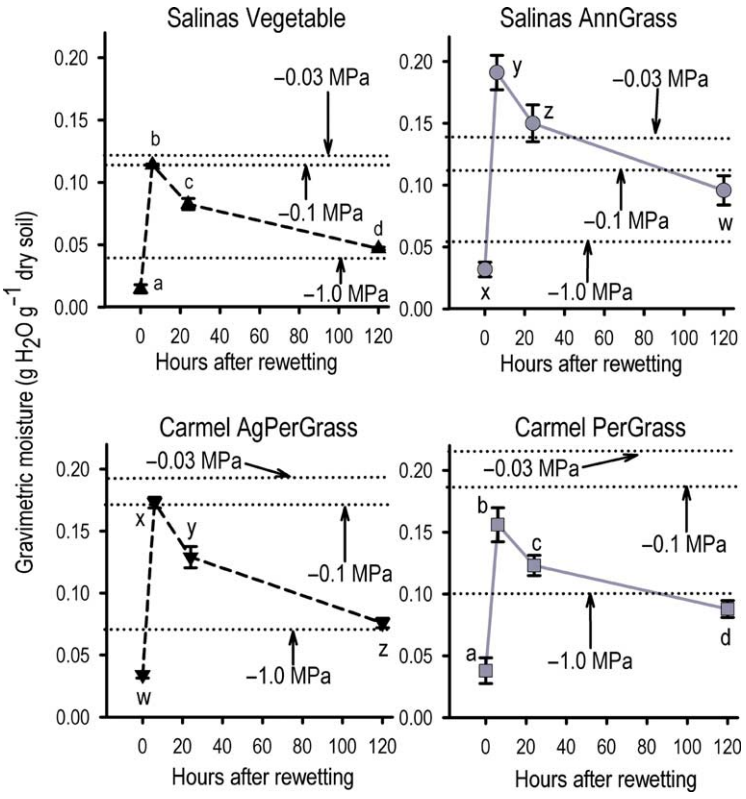

Fig. 1. Temporal changes in gravimetric water content of ecosystems in Salinas and Carmel Valleys. Dotted horizontal lines indicate soil water potentials that correspond to a given soil moisture. For a given site, points with different letters are significantly different from others (Nested GLM, $P<0.05$, and post-hoc Tukey's test, $n=4$, mean $\pm$ SE at each time point).

biomass than Carmel Valley sites, which can be attributed to the larger biomass of 'Salinas AnnGrass'. Plant biomass was greater in the grassland than agricultural site of each valley pair, and species diversity, richness, and evenness were greatest in the grasslands.

3.2. C and N dynamics in Salinas Valley annual ecosystems

Soil moisture changed significantly after rewetting in both Salinas Valley sites (Fig. 1). Prior to rewetting, gravimetric soil moisture was similar in the 'Salinas Vegetable' and 'Salinas AnnGrass' soils; for both soils, soil water potential (Ψ_s) was about -1.0 MPa. During rewetting, water pooled on the 'Salinas AnnGrass' soil surface, which had a dense, hydrophobic mat of dead roots and root litter that is typically present in annual grasslands. 'Salinas AnnGrass' had greater gravimetric soil moisture than 'Salinas Vegetable' ($P<0.05$) and tended to have higher Ψ_s.

Microbial biomass C did not change significantly with time in either Salinas Valley site in response to the addition of water (Tables 4 and 5). MBC in 'Salinas AnnGrass' was 1.5-fold greater than in the 'Salinas Vegetable' soil ($P<0.05$). Total PLFA was approximately 7-fold higher in the 'Salinas AnnGrass' than 'Salinas Vegetable' soil.

Table 4
Nested GLM of nitrogen and carbon variables and specific PLFA

	Valley[a]	Time	Ecosystem (Valley)	Ecosystem[x] Time (Valley)
C-variables				
Microbial biomass C[b]	*	NS	****	NS
Total PLFA	**	NS	****	NS
Microbial respiration[b]	NS	****	****	***
CO_2-C efflux[b]	****	****	****	****
N-variables				
NO_3-N	***	NS	****	NS
NH_4-N[b]	NS	NS	**	NS
Net mineralizable N[b]	**	NS	****	NS
N_2O-N efflux[b]	NS	****	NS	NS
NO-N efflux[b]	NS	*	***	NS
PLFAs				
18:1ω9c	NS	NS	****	*
16:1ω5c	*	NS	****	NS
Branched PLFA	**	NS	***	NS
10Me	***	NS	****	NS
17cy:pre[b]	****	*	****	NS
Monounsaturated: saturated	*	NS	****	****

*$P<0.05$, **$P<0.01$, ***$P<0.001$, ****$P<0.0001$, NS = not significant.
[a] 'Valley' refers to Carmel or Salinas Valleys. 'Ecosystem' refers to grassland or agricultural ecosystem. 'Time' refers to 0, 6, 24 or 120 h after rewetting.
[b] Data have been transformed by $\ln(x+1)$.

Table 5
Means and standard errors of nitrogen and carbon variables and specific PLFAs according to ecosystem ($n=16$) (Nested GLM, $P<0.05$, and post-hoc Tukey's test)

	Salinas Valley				Carmel Valley			
	Salinas Vegetable		Salinas AnnGrass		Carmel AgPerGrass		Carmel PerGrass	
	x	±SE	x	±SE	x	±SE	x	±SE
Carbon								
MBC[a] ($\mu g\ g^{-1}$)	4.02*	0.18	5.87	0.23	4.83*	0.18	6.01	0.13
Total PLFA ($\mu g\ g^{-1}$)	5.78*	0.76	42.28	3.24	26.04*	1.86	42.28	3.24
Resp.[a] ($\mu g\ C\ g^{-1}\ h^{-1}$)	0.52*	0.07	1.58	0.24	0.78*	0.47	1.26	0.14
CO_2-C[a] ($mg\ m^{-2}\ h^{-1}$)	0.43*	0.18	2.26	0.48	2.24	0.47	2.46	0.52
Nitrogen								
NO_3-N ($\mu g\ g^{-1}$)	7.69*	1.64	76.85	4.98	44.97*	4.31	13.67	2.04
NH_4-N[a] ($\mu g\ g^{-1}$)	0.07*	0.03	1.82	0.23	1.68	0.18	1.41	0.21
Net min. N[a] ($\mu g\ g^{-1}$)	0.52*	0.13	3.96	0.07	1.83*	0.26	3.40	0.11
NO-N ($\mu g\ m^{-2}\ h^{-1}$)	0.02*	0.01	1.35	0.29	1.05	0.19	0.91	0.21
N_2O-N[a] ($\mu g\ m^{-2}\ h^{-1}$)	1.67	0.45	1.47	0.48	1.66	0.48	2.30	0.37
PLFA								
16:1ω5c ($\mu g\ g^{-1}$)	0.190*	0.025	1.281	0.092	0.384*	0.040	0.781	0.061
Branched ($\mu g\ g^{-1}$)	1.528*	0.190	11.404	0.793	2.812*	0.190	6.974	0.367
10Me ($\mu g\ g^{-1}$)	0.473*	0.053	3.095	0.232	2.812*	0.189	1.926	0.089
18:1ω9c ($\mu g\ g^{-1}$)	0.469*	0.059	3.812	0.000	0.838*	0.058	3.022	0.340
17cy:pre[a]	0.299*	0.010	0.484	0.009	0.535*	0.019	0.453	0.011
Monounsat.: Sat.	1.077*	0.037	0.942	0.016	0.953*	0.017	1.158	0.028

See Table 2 for level of significance, and for differences between valleys. Asterisks indicate that means are significantly different between ecosystems in each valley.
[a] Data have been transformed by $\ln(x+1)$.

Soil respiration increased immediately after rewetting and was 3-fold greater in 'Salinas AnnGrass' than 'Salinas Vegetable' (Tables 4 and 5; Fig. 2). Only 'Salinas AnnGrass' maintained a significantly elevated soil respiration rate after rewetting through the entire experiment. Carbon dioxide efflux increased more strongly after rewetting in the annual grassland than agricultural soil. In 'Salinas AnnGrass', CO_2-C efflux at 6 h after rewetting reached its greatest rate and then declined gradually through time. In contrast, a delayed and much smaller increase occurred in the 'Salinas Vegetable' soil.

Inorganic N pools and potential net mineralizable N showed little or no significant change in the Salinas Valley soils (Tables 4 and 5). Soil $NO_3^- - N$ was 10-fold greater in 'Salinas AnnGrass' than 'Salinas Vegetable'. Soil $NH_4^+ - N$ was present at lower concentrations than $NO_3^- - N$, but it was approximately 25 times greater in 'Salinas AnnGrass' than 'Salinas Vegetable'. Net mineralizable N in the 'Salinas AnnGrass' soil was almost eight times greater than in 'Salinas Vegetable'.

Soil effluxes of N_2O-N increased to peak rates immediately after rewetting, and then decreased to pre-rewetting rates in both 'Salinas AnnGrass' and 'Salinas Vegetable' (Fig. 3). The NO-N flux of 'Salinas AnnGrass' was 75-fold greater than the flux observed from the 'Salinas Vegetable' soil at 6 h after rewetting. The 'Salinas AnnGrass' soil maintained this rate of NO-N efflux until the termination of the experiment. Linear regression of N_2O-N with gravimetric water content was significant for both sites ($r^b=0.45$ for 'Salinas AnnGrass', $r^b=0.29$ for 'Salinas Vegetable'; $P<0.05$), but linear regression of NO-N and N_2O-N with $\mu g\ NO_3^- - N\ m^{-2}$ was not significant (data not shown).

3.3. C and N dynamics in Carmel Valley perennial ecosystems

Gravimetric soil moisture (Fig. 1) was never significantly different between the Carmel Valley sites ($P<0.05$). In both 'Carmel PerGrass' and 'Carmel AgPerGrass', Ψ_s was approximately -1.5 to -2 MPa prior to rewetting. Water infiltrated readily in both soils, and no restrictive layers appeared to be present. 'Carmel AgPerGrass' tended to have slightly higher Ψ_s even though gravimetric water content was not significantly different between sites.

Microbial biomass, as measured by either chloroform-fumigation and extraction or total PLFA, did not change significantly with time after rewetting in both Carmel Valley sites (Tables 4 and 5). MBC and total PLFA were 1.3–3 times greater in 'Carmel PerGrass' than 'Carmel AgPerGrass' soil.

Soil respiration increased immediately after rewetting in both soils and remained higher than initial values through the rest of the experiment (Tables 4 and 5; Fig. 2), although the 'Carmel PerGrass' soil respired almost twice as much CO_2-C as 'Carmel AgPerGrass'. Soil CO_2-C efflux in both sites increased rapidly in response to rewetting, but the response of the 'Carmel

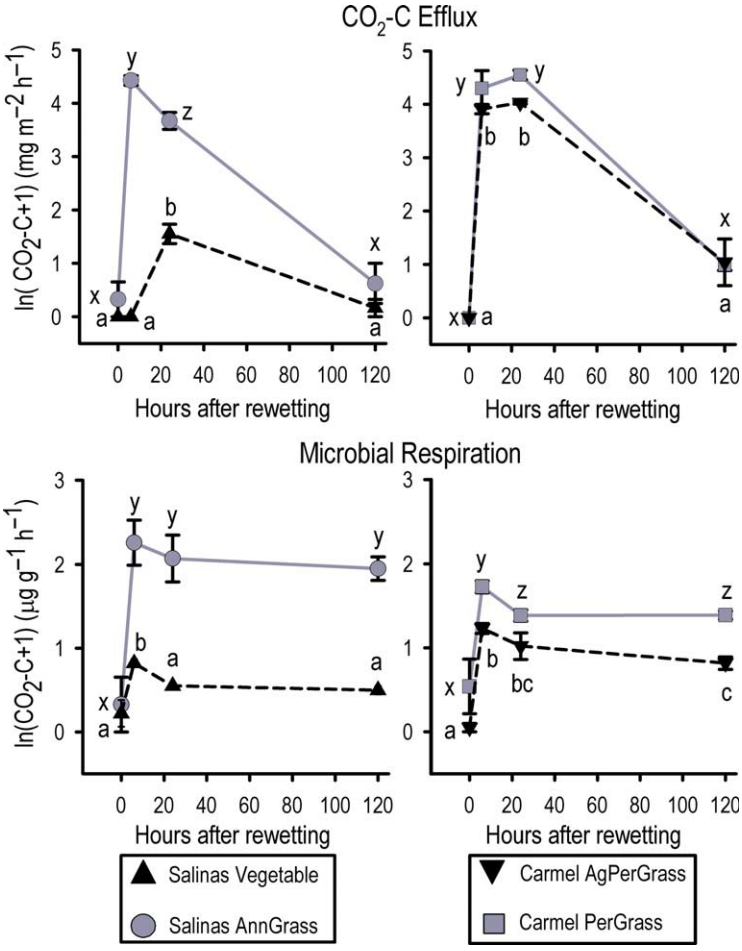

Fig. 2. Temporal changes in carbon dioxide efflux and microbial respiration from ecosystems in Salinas and Carmel Valleys. For a given site, points with different letters are significantly different from others (Nested GLM, $P<0.05$, and post-hoc Tukey's test, $n=4$, mean $\pm$ SE at each time point).

AgPerGrass' tended to be somewhat lower than that of 'Carmel PerGrass'. Elevated rates occurred in both sites between six and 24 h and then declined from 24 to 120 h after rewetting.

Inorganic N pools and net mineralizable N of both Carmel Valley sites did not respond to rewetting (Tables 4 and 5). Soil $NO_3^- - N$ of 'Carmel AgPerGrass' was approximately 3-fold greater than in 'Carmel PerGrass', which may be attributable to the fertilizer applied by the grower ($\sim$27 kg N ha^{-1}) just before the intact soil cores were extracted. No significant differences in $NH_4^+ - N$ were found between sites, although it was present at much lower concentrations than $NO_3^- - N$ in both Carmel Valley sites. Net mineralizable N was almost 2-fold greater in 'Carmel PerGrass' than 'Carmel AgPerGrass'.

The flux of N_2O-N increased 2.5-fold in 'Carmel PerGrass' after rewetting (Fig. 3). In 'Carmel AgPerGrass', N_2O-N increased from undetectable amounts to similar rates as in 'Carmel PerGrass' soil between 0 and 6 h after rewetting. The efflux in both sites then declined to pre-wetting rates thereafter. Efflux of NO-N from 'Carmel PerGrass' soil increased between 0 and 6 h after rewetting. While NO-N efflux did not change significantly in 'Carmel PerGrass', the magnitude of the NO-N efflux tended to be similar for the grassland and agricultural soils. Linear regression of N_2O-N with gravimetric water content was significant for each site ($r^b=0.31$ for 'Carmel PerGrass', $r^b=0.43$ for 'Carmel AgPerGrass'; $P<0.05$), but linear regression of NO-N and N_2O-N with μg NO_3-N m^{-2} was not significant (data not shown).

3.4. Microbial community composition

Sites were analyzed separately to better detect temporal differences using a CCA constrained for time since rewetting (Fig. 4). The first two axes of the CCA explained 63.1% of the variation in PLFA in 'Salinas Vegetable', followed by 55.9% in 'Carmel PerGrass', 25.3% in 'Carmel AgPerGrass', and 22.6% in 'Salinas AnnGrass'. PLFA profiles that were sampled in dry soils before rewetting (0 h) differed significantly from those after rewetting in the 'Carmel PerGrass' and 'Salinas Vegetable' soils (Monte Carlo tests, $P<0.05$). PLFA profiles measured in dry soil from 'Carmel AgPerGrass' were slightly but not significantly different (0 h, $P=0.06$) from profiles in the wetter soils. The microbial community

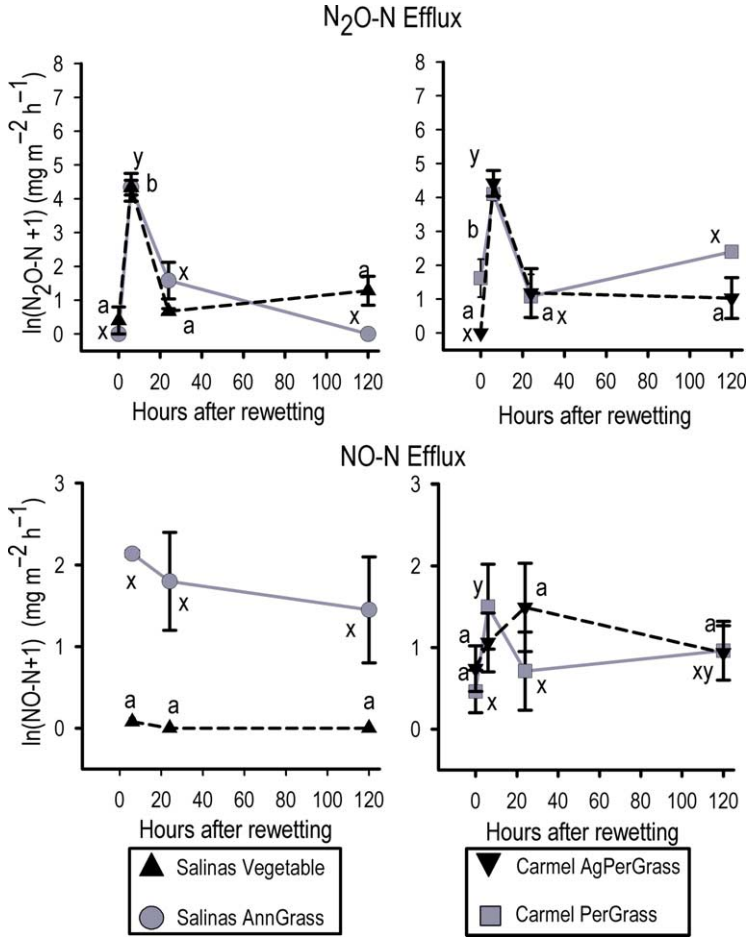

Fig. 3. Temporal changes in nitrous oxide efflux and nitric oxide efflux from ecosystems in Salinas and Carmel Valleys. For a given site, points with different letters are significantly different from others (Nested GLM, $P<0.05$, and post-hoc Tukey's test, $n=4$, mean $\pm$ SE at each time point).

of 'Salinas Vegetable' soil responded most strongly to rewetting; not only was its composition in driest soil significantly different from other sampling times, but later samples (i.e. 6 and 24 h) also were considerably different from each other (Monte Carlo, $P<0.05$). Microbial communities in 'Salinas AnnGrass' did not show a response to rewetting.

In the CCA analyses, specific PLFA were positively associated with microbial communities at certain times after rewetting. All PLFA mentioned below had loading scores greater than 1.0, and were associated with times that were significant in explaining variation in the PLFA data set.

In 'Salinas Vegetable', actinomycetes (i.e. tbsa 10me18:0, 17:0 10Me) (Kroppenstedt, 1985), and Gram-negative bacteria (i.e. 16:1 2OH) (Federle, 1986; Ludvigsen et al., 1999) had relatively higher abundances before rewetting. Six hours after rewetting, 17:0 anteiso and 16:0 10Me were positively associated with microbial communities. Fungal and general eukaryotic markers (i.e. a mixture of 18:1 ω7c, 18:1 ω9t, 18:1 ω12t and 18:1 ω9c), Gram-negative bacteria (i.e. 16:1 ω7c), 15:0 anteiso, and general bacterial markers (i.e. 14:0) (Tunlid and White, 1992; Myers et al., 2001) were positively associated with microbial communities at 24 h after rewetting. 16:1 ω5c, also associated with microbial communities 24 h after rewetting, is found in some bacteria (Olsson, 1999).

In 'Carmel PerGrass', fungal markers (i.e. a mixture of 18:0 anteiso and 18:2 ω6,9c; 18:1 ω9c), a mixture of two unknowns and 19:0cy ω10c had high positive loading scores along Axis 1 before rewetting. After rewetting, microbial communities of 'Carmel PerGrass' had relatively greater abundances of PLFA markers for Gram-positive bacteria (i.e.16:0 iso) (O'Leary and Wilkinson, 1988), and actinomycetes (i.e. tbsa 10me18:0; 17:0 10Me) (Kroppenstedt, 1985). 17:0 10Me has also been identified as an anaerobic bacterial marker (Vestal and White, 1989). In 'Carmel AgPerGrass', Gram-negative bacteria (i.e.16:1 2OH) (Federle, 1986; Ludvigsen et al., 1999), fungal markers (i.e. 18:0 anteiso and 18:2 ω6,9c) (Federle, 1986; Myers et al., 2001), general bacterial markers (i.e. 14:0) (Tunlid and White, 1992; Myers et al., 2001), and 15:0 iso had relatively greater abundances in microbial communities before rewetting than after rewetting. Other eukaryotic and fungal markers (i.e. 18:1 ω7c, 18:1 ω9t, 18:1 ω12t and 18:1 ω9c), and a possible sulfate reducer (i.e. 17:1 iso) (Macalady et al., 2000) tended to have greater abundances

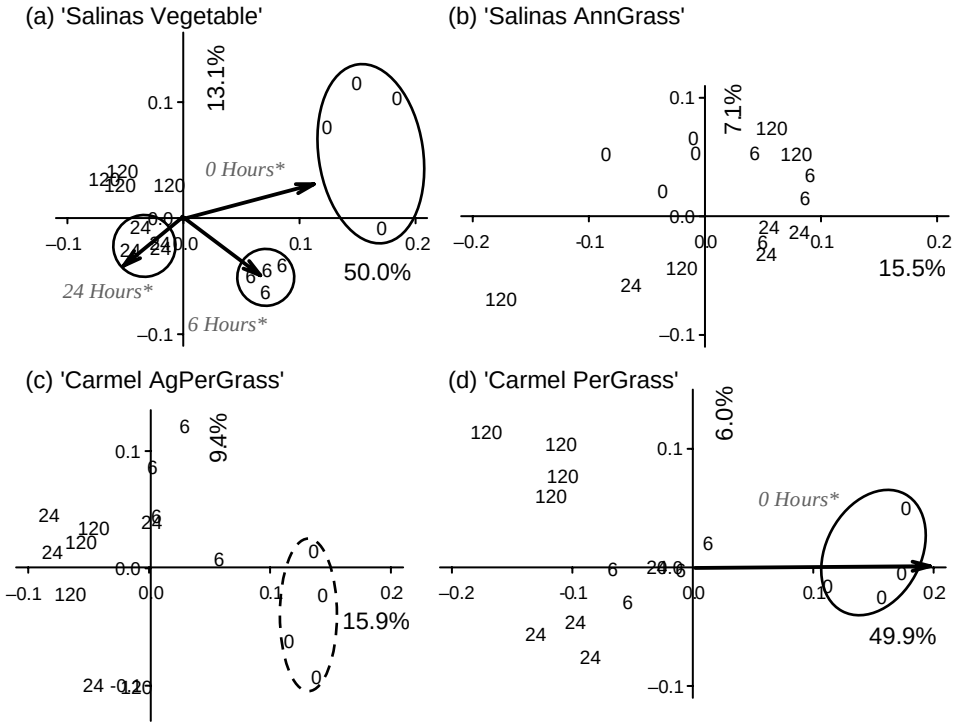

Fig. 4. (a–d) CCAs of soil microbial community composition of ecosystems in Salinas and Carmel Valleys. Microbial communities for a given time are indicated by a number, e.g. microbial communities at 6 h after rewetting are represented by '6'. Times that are significant in explaining variation in the microbial community composition are indicated by vectors (Monte Carlo, $P<0.05$). Ellipses distinguish soil microbial communities that are associated with vectors. In (c), the ellipse is formed with a dashed line because the vector associated with soil microbial communities at time zero approaches significance (Monte Carlo, $P=0.06$).

in microbial communities after, rather than before, rewetting.

When individual PLFA markers were analyzed by ecosystem within each valley with ANOVA, grasslands were different from cultivated sites and some temporal responses to rewetting were observed (Tables 4 and 5). In most cases, concentrations and ratios of specific markers were greater for the Salinas Valley, but this was attributed to the high values in 'Salinas AnnGrass'. However, the ratio 17cy:pre was greater in the Carmel Valley compared to Salinas Valley, and the fungal marker 18:1 ω9c was not significantly different. In both valleys, the grasslands had greater values for specific PLFA markers than their counterpart agricultural ecosystem. This was true in all cases, except the sum of 10Me PLFA and 17cy:pre. Both were greater in 'Carmel AgPerGrass' than 'Carmel PerGrass'. Also, the proportion of monounsaturated:saturated PLFA was greater in 'Salinas Vegetable' than in 'Salinas AnnGrass', while in 'Salinas AnnGrass' the proportion was relatively even. The interaction of Ecosystem*Time (Valley) was significant (Table 4) for the ratio of monounsaturated:saturated PLFA, indicating that the ecosystems in each valley responded distinctly from each other. The ratio of monounsaturated:saturated PLFA decreased significantly after rewetting for 'Carmel PerGrass' and increased for 'Salinas Vegetable'. It remained constant for the 'Salinas AnnGrass' and 'Carmel AgPerGrass' (Fig. 5). The ratio of 17 cy:pre (16:1ω7c), was significant for time (Table 4), and decreased immediately after rewetting in the 'Salinas AnnGrass' and 'Salinas Vegetable', but not in the other soils (Fig. 5). The fungal marker 18:1ω9c decreased after rewetting only in 'Carmel PerGrass' (Fig. 6).

Estimates of microbial diversity indicated that both grassland ecosystems had greater diversity than their agricultural counterparts. Grassland ecosystems had approximately 1.5–2-fold more individual PLFA than the agricultural ecosystems ($n=4$, $P<0.05$). The number of PLFA detected in 'Salinas Vegetable' was 23.2 ± 0.8 while in 'Salinas AnnGrass', the number of detected PLFA was 42.8 ± 0.7. In 'Carmel AgPerGrass', the number was 28.5 ± 1.4, and in 'Carmel PerGrass' it was 43.3 ± 2.5.

Thus, the temporal differences in microbial community composition and in specific PLFA that were observed after soil rewetting were different between sites, and were only obvious when the overriding effects of land use history were not included in the analysis.

4. Discussion

Unlike other soil rewetting experiments (Sparling and Ross, 1988; Appel, 1998; Pulleman and Tietema, 1999; Lundquist et al., 1999a,b), soil inorganic N, net mineralizable N, MBC and total PLFA showed little or no response to

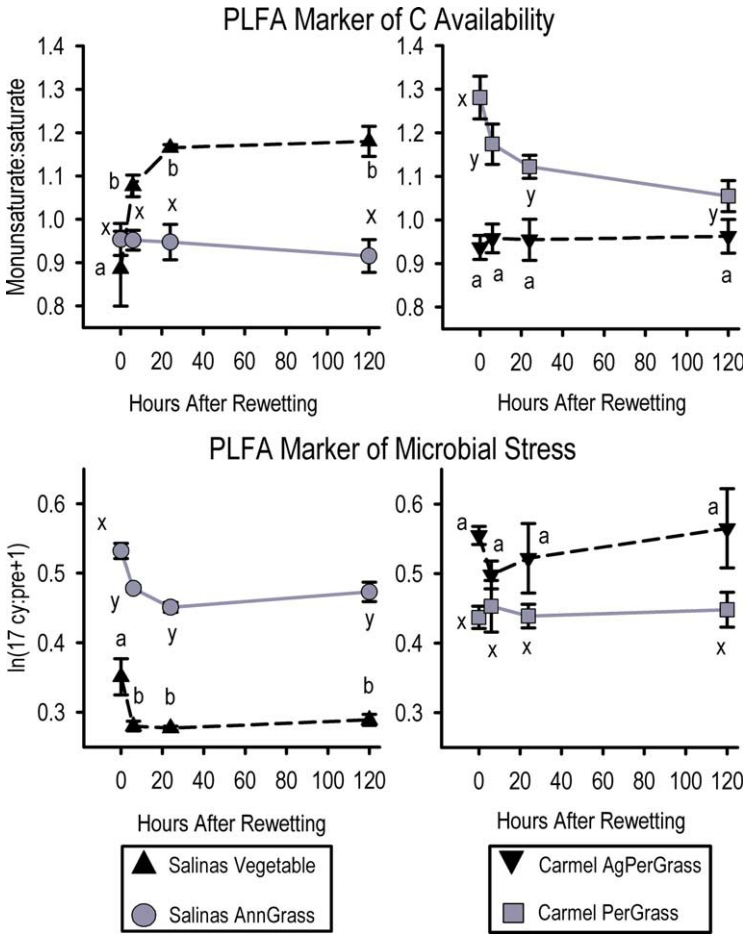

Fig. 5. Temporal changes in PLFA markers for C availability and microbial stress in ecosystems in Salinas and Carmel Valleys. For a given site, points with different letters are significantly different from others (Nested GLM, $P<0.05$, and post-hoc Tukey's test, $n=4$, mean $\pm$SE at each time point).

the application of water. Although the absence of microbial biomass response to rewetting opposes other findings, it was consistent with a study that showed a high stability of microbial biomass at 24 h after a mild rewetting of dry soils (Potthoff et al., 2001). Also, our rewetting event was not as extreme as other studies (van Gestel et al., 1993a; Appel, 1998; Magid et al., 1999; Franzluebbers et al., 2000). For example, van Gestel et al. (1993a) observed increases in

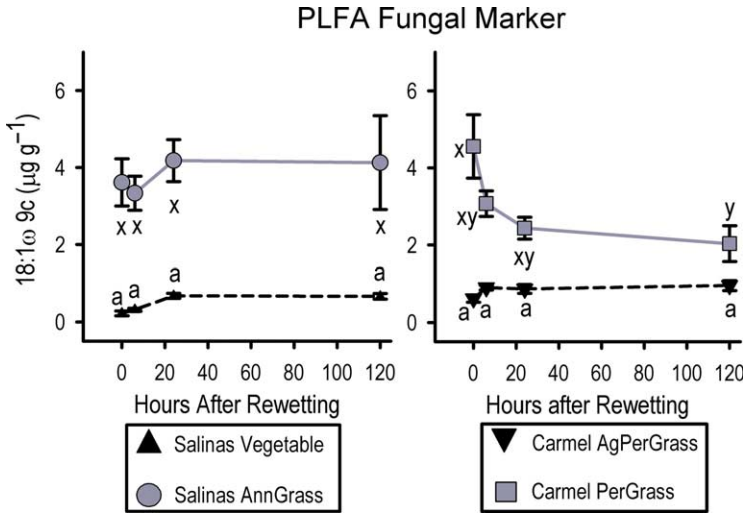

Fig. 6. Temporal changes in a fungal PLFA marker in ecosystems in Salinas and Carmel Valleys. For a given site, points with different letters are significantly different from others (Nested GLM, $P<0.05$, and post-hoc Tukey's test, $n=4$, mean $\pm$SE at each time point).

MBC after rewetting, but the soils were first dried at 40 °C to much less than −10 MPa prior to rewetting. Our soils were dried at 25 °C to represent the mild spring conditions in the Central Coast of California, and the driest water potentials were approximately −1.5 MPa. Nonetheless, our experiment demonstrates that important changes can take place in microbial activity, gas efflux and community composition during mild wet/dry cycles.

4.1. Microbial respiration and CO_2-C efflux from soil

Grassland ecosystems had greater soil respiration rates immediately after rewetting than their counterpart agricultural ecosystems. They maintained elevated rates, possibly due to greater availability of labile C after rewetting (van Gestel et al., 1993a,b; Lundquist et al., 1999a; Franzluebbers et al., 2000). Greater amounts of available C in grassland soils can be attributed to higher SOM and microbial biomass, differences in rooting densities and rhizodeposition before core collection, or decomposition of roots during the period of soil equilibration. The 'Salinas Vegetable' soil had the lowest respiration rates, which corresponded to its low MBC and total soil C.

In part, increases in CO_2-C efflux immediately after rewetting were due to the displacement of in situ CO_2-C in the soil pores by the influx of water (Hillel, 1982; Calderón et al., 2002). Thereafter, soil CO_2-C efflux in the grassland ecosystems and 'Carmel PerGrass' likely was indicative of continued microbial respiration, e.g. from particulate organic matter released from slaked aggregates (Denef et al., 2001). In contrast, 'Salinas Vegetable', the most disturbed soil, had minimal CO_2-C efflux and respiration rates after 24 h, probably because substrate availability and lower pools of labile C limited microbial activity.

4.2. Nitrogen dynamics

Efflux of trace N gases was expected to correspond to differences in soil inorganic N and potential net mineralizable N (Davidson et al., 2000) between grassland and agricultural ecosystems, but the data did not show a direct relationship among these variables. Nitrification was a probable source of trace N_2O gas production because water-filled pore space was lower than that expected for high N_2O loss via denitrification, i.e. it was between 50–60% in the annual grassland soil and 35–50% in the other soils during the short period of high N_2O efflux (Paul and Clark, 1996; Schjønning et al., 2003). Although nitrification may have occurred at high rates in the grassland and agricultural ecosystems based on N_2O effluxes, NO_3^- − N concentrations would not necessarily have been expected to increase. Instead, NO_3^-−N may have been rapidly consumed by microbial immobilization (Jackson et al., 1989; Burger and Jackson, 2003), and small increases may not have been detectable due to the large ambient NO_3^-−N pools.

The highest NO efflux was in the annual grassland, which tended to have the highest potential net mineralizable N. Rates of NO efflux in the grasslands were within the range of annual grassland soils measured by Davidson et al. (1992). High NO efflux is often associated with high rates of potential net mineralization (Davidson et al., 2000) or net nitrification (Stark et al., 2000) and can occur by abiotic reaction of HNO_2^-/NO_2^- to NO (Venterea and Rolston, 2000). Large variation between the cores in this study also suggests that 'hotspots' of activity exist (Christensen et al., 1990), especially in the grassland soils.

4.3. Microbial community composition

As land use intensification increases, soil microbial diversity may decrease, and microbial activity and the resistance of community composition in response to a perturbation may be compromised (Swift et al., 1996). Microbial activity (i.e. respiration, potential N mineralization) and labile C and N pools (i.e. inorganic N, MBC, total PLFA) in the agricultural ecosystems were lower in comparison to their paired grassland ecosystems, suggesting that land use intensification had degraded soil quality. Agricultural soils had lower microbial diversity than grassland ecosystems in both valleys, as estimated by fewer PLFA that were detected in the agricultural ecosystems. Therefore, agricultural soils would be expected to display lower resilience and resistance in response to soil rewetting. Indeed, microbial communities in both agricultural ecosystems exhibited alterations in composition after rewetting. This was most distinct in 'Salinas Vegetable', the most intensively managed agricultural ecosystem. Its microbial communities differed at 0, 6, and 24 h after rewetting, while microbial communities of 'Carmel AgPerGrass' tended to differ only before rewetting and were similar at the sampling times afterward. In contrast, 'Salinas AnnGrass' supported high microbial diversity compared to 'Salinas Vegetable' and displayed increases in microbial activity, but did not have significant changes in microbial community composition. This suggests that microbial communities of less disturbed ecosystems like grasslands may be dynamic in terms of functional responses to a perturbation but more resistant to changes in community composition. The response of 'Carmel PerGrass', the undisturbed relict perennial grassland, contradicts this argument because both microbial activity and community composition changed in response to rewetting. One hypothesis is that differences in plant community composition and diversity or life form (e.g. perennial bunchgrasses vs. annual grasses) in these grasslands may influence the response of the microbial communities, whereas agricultural management practices like irrigation, tillage, and external soil amendments may have an overriding effect on soil microorganisms in agricultural ecosystems (Buckley and Schmidt, 2001; Steenwerth et al., 2003).

Patterns in microbial community composition in response to rewetting may also be related to soil C availability. A purported indicator of C availability, the ratio of

monounsaturated to saturated PLFA (Guckert et al., 1986; Kieft et al., 1994, 1997), increased in 'Salinas Vegetable' soil after rewetting, suggesting that an influx of C sources was provided to the microorganisms upon rewetting. Even so, low respiration rates in 'Salinas Vegetable' soil compared to 'Salinas AnnGrass' indicate that C availability in 'Salinas Vegetable' was relatively limited. This ratio remained constant for 'Salinas AnnGrass' and 'Carmel AgPerGrass', indicating less change in C availability to microbes in these soils. Unexpectedly, the ratio decreased significantly immediately after rewetting in the 'Carmel PerGrass' soil despite elevated respiration rates at all times after rewetting. Changes in this ratio may also reflect leaching of soluble C below 6 cm. Alternatively, the ratio may reflect the activity of various populations more than actual C availability because land use history affects the composition of the microbial community.

Irrigated agricultural soils typically have consistently more available water to support crops than grassland soils, which, in a Mediterranean climate, would be dry in the summer. Agricultural soils might then be expected to exhibit more stress during a wet–dry cycle. In fact, a PLFA biomarker for microbial stress, the ratio of 17 cy:pre (16:1ω7c) (Kieft et al., 1994; Kieft et al., 1997), decreased markedly after rewetting in the 'Salinas Vegetable' and 'Salinas AnnGrass'. No change was observed in 17 cy:pre in 'Carmel AgPerGrass' and 'Carmel PerGrass'. Thus, microbial communities in irrigated agricultural soils do not appear to be less acclimated to the stress of wet/dry cycles than their grassland counterparts.

In the agricultural ecosystems, some similarities in the changes in relative abundances of specific PLFA markers in microbial communities before and after rewetting occurred. In both agricultural ecosystems, markers for Gram-negative bacteria were relatively higher in the drier soils prior to rewetting, but markers for general eukaryotes and fungi increased following rewetting. These trends were not observed for 'Carmel PerGrass'. In fact, a slightly different assemblage of fungal markers was relatively higher before rewetting than afterwards. No significant changes were observed for 'Salinas AnnGrass', which was shown in previous studies to be substantially different from relict perennial grasslands (Steenwerth et al., 2003). Thus, consistent changes in microbial communities and their responses to a mild rewetting event are not evident across land use types from this study. Differences in the response of microbial communities of each ecosystem may be related to both specific environmental conditions and interactions of microbes with other soil biota in response to disturbance.

4.4. Conclusion

Although this study included few sites, the ecosystems and their microbial communities were representative of those of these land use types in the Carmel and Salinas Valleys (Steenwerth et al., 2003). Within this subset, the results suggest that land use intensification decreases microbial diversity, increases the magnitude of change in the microbial community after soil rewetting, and reduces microbial activity and soil C and N availability in response to increased moisture. In less disturbed ecosystems, rewetting tended to increase the activity of soil microorganisms compared to tilled agricultural systems, but with less consistent effects on temporal change in the microbial community composition. Agricultural intensification thus appears to decrease the resistance of soil microbial community composition to change after rewetting, thereby reducing its stability. This reduction in stability is associated with lower ecosystem function, i.e. lower soil microbial activity, compared to grassland soils.

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References

Appel, T., 1998. Non-biomass soil organic N – the substrate for N mineralization flushes following soil drying-rewetting and for organic N rendered $CaCl_2$-extractable upon soil drying. Soil Biology & Biochemistry 30, 1445–1456.

Barrett, J.E., Burke, I.C., 2000. Potential nitrogen immobilization in grassland soils across a soil organic matter gradient. Soil Biology & Biochemistry 32, 1707–1716.

Bligh, E.G., Dyer, W.M., 1959. A rapid method of lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 35, 911–917.

Bossio, D.A., Scow, K.M., 1995. Impact of carbon and flooding on the metabolic diversity of microbial communities in soils. Applied and Environmental Microbiology 61, 4043–4050.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology & Biochemistry 17, 837–842.

Buckley, D.H., Schmidt, T.M., 2001. The structure of microbial communities in soil and the lasting impact of cultivation. Microbial Ecology 42, 11–21.

Burger, M., Jackson, L.E., 2003. Microbial immobilization of ammonium and nitrate in relation to ammonification and nitrification rates in organic and conventional cropping systems. Soil Biology & Biochemistry 35, 29–36.

Calderón, F.J., Jackson, L.E., 2002. Roto-tillage, disking and subsequent irrigation: effects on soil nitrogen dynamics, microbial biomass and carbon dioxide efflux. Journal of Environmental Quality 31, 752–758.

Calderón, F.J., Jackson, L.E., Scow, K.M., Rolston, D.E., 2000. Microbial responses to simulated tillage in cultivated and uncultivated soils. Soil Biology & Biochemistry 32, 1547–1559.

Christensen, S., Simkins, S., Tiedje, J.M., 1990. Temporal patterns of soil denitrification; their stability and causes. Soil Science Society of America Journal 54, 1614–1618.

Cook, T.D., 1978. Soil survey of Monterey County, California. United States Department of Agriculture, Soil Conservation Service, US Forest Service and University of California Agricultural Experiment Station, Washington, DC pp. 15–16, 34, 224–225.

Davidson, E.A., 1992. Sources of nitric oxide and nitrous oxide following wetting of dry soil. Soil Science Society of America Journal 56, 95–102.

Davidson, E.A., Keller, M., Erickson, H.E., Verchot, L.V., Veldkamp, E., 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides. Bioscience 50, 667–680.

Denef, K., Six, J., Bossuyt, H., Frey, S.D., Elliot, E.T., Merckx, R., Paustian, K., 2001. Influence of dry–wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biology & Biochemistry 33, 1599–1611.

Federle, T.W., 1986. Microbial distribution in soil. In: Megusar, F., Gantar, M. (Eds.),. Perspectives in Microbial Ecology, Slovene Society for Microbiology, Ljublana, pp. 493–498.

Folorunso, O.A., Rolston, D.E., 1984. Spatial variability of field-measured denitrification gas fluxes. Soil Science Society of America Journal 48, 1214–1219.

Franzluebbers, A.J., Haney, R.L., Honeycutt, C.W., Schomberg, H.H., Hons, F.M., 2000. Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. Soil Biology & Biochemistry 64, 613–623.

Gee, G.W., Bauder, J.W., 1979. Particle size analysis by hydrometer: a simplified method for routine textural analysis and a sensitivity test of measurement parameters. Soil Science Society of America Journal 43, 1004–1007.

Guckert, J.B., Hood, M.A., White, D.C., 1986. Phospholipid ester-linked fatty acid profile changes during nutrient deprivation of *Vibrio cholerae*: increases in trans/cis ratio in proportions of cyclopropyl fatty acids. Applied and Environmental Microbiology 52, 794–801.

Hickman, J.C., 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley.

Hillel, D., 1982. Introduction to Soil Physics. Academic Press, San Diego, USA pp. 364.

Jackson, L.E., Schimel, J.P., Firestone, M.K., 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. Soil Biology & Biochemistry 21, 409–415.

Joergensen, R.G., 1996. The fumigation extraction method to estimate soil microbial biomass: calibration of the k_{EC}-factor. Soil Biology & Biochemistry 28, 25–31.

Kent, M., Coker, P., 1992. Vegetation description and analysis: a practical approach. John Wiley, Chichester pp. 95–97.

Kieft, T., Soroker, E., Firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biology & Biochemistry 19, 119–126.

Kieft, T., Ringelberg, D.B., White, D.C., 1994. Changes in ester-linked phospholipid fatty acid profiles of subsurface bacteria during starvation and desiccation in a porous medium. Applied and Environmental Microbiology 60, 3292–3299.

Kieft, T.L., Wilch, E.O., O'Connor, K., Ringelberg, D.B., White, D.C., 1997. Survival and phospholipid fatty acid profiles of surface and subsurface bacteria in natural sediment microcosms. Applied and Environmental Microbiology 63, 1531–1542.

Kroppenstedt, R.M., 1985. Fatty-acid and menaquinone analysis of actinomycetes and related organisms. In: Goodfellow, M., Minnikin, D.E. (Eds.), Society for applied bacterial systematics, meeting, Edinburgh, Scotland, July, 1983. Academic Press, Orlando, pp. 173–200.

Lal, R., 2002. Soil carbon dynamics in cropland and rangeland. Environmental Pollution 116, 353–362.

Ludvigsen, L., Albrechtsen, H.-J., Ringelberg, D.B., Ekelund, F., Christensen, T.H., 1999. Distribution and composition of microbial populations in a landfill leachate contaminated aquifer (Grindsted Denmark). Microbial Ecology 37, 197–207.

Lundquist, E.J., Jackson, L.E., Scow, K.M., 1999a. Wet–dry cycles affect dissolved organic carbon in two California agricultural soils. Soil Biology & Biochemistry 31, 1031–1038.

Lundquist, E.J., Scow, K.M., Jackson, L.E., Uesugi, S.L., Johnson, C.R., 1999b. Rapid response of soil microbial communities from conventional, low input, and organic farming systems to a wet/dry cycle. Soil Biology & Biochemistry 31, 1661–1675.

Macalady, J.L., Mack, E.E., Nelson, D.C., Scow, K.M., 2000. Sediment microbial community structure and mercury methylation in mercury-polluted Clear Lake, California. Applied and Environmental Microbiology 66, 1479–1488.

Magid, J., Kjærgaard, C., Gorissen, A., Kuikman, P.J., 1999. Drying and rewetting of a loamy sand soil did not increase the turnover of native organic matter, but retarded the decomposition of added ^{14}C-labelled plant material. Soil Biology & Biochemistry 31, 595–602.

Meixner, F.X., Fickinger, Th., Marufu, L., Serça, D., Nathaus, F.J., Makina, E., Mukurumbira, L., Andreae, M.O., 1997. Preliminary results on nitric oxide emission from a southern African savanna ecosystem. Nutrient Cycling in Agroecosystems 48, 123–138.

Myers, R.T., Zak, D.R., White, D.C., Peacock, A., 2001. Landscape-level patterns of microbial composition and substrate use in upland forest ecosystems. Soil Science Society of America Journal 65, 359–367.

O'Leary, W.M., Wilkinson, S.G., 1988. Gram-positive bacteria. In: Ratledge, C., Wilkinson, S.G. (Eds.), Microbial Lipids. Academic Press, London, pp. 117–201.

Olsson, P.A., 1999. Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. FEMS Microbiology Ecology 29, 303–310.

Panek, J.A., Matson, P.A., Ortiz-Monasterio, I., Brooks, P., 2000. Distinguishing nitrification and denitrification sources of N_2O in a Mexican wheat system using ^{15}N. Ecological Applications 10, 506–514.

Paul, E.A., Clark, F.E., 1996. Soil Biology and Biochemistry, Second ed. Academic Press, San Diego pp. 204.

Pella, E., 1990. Elemental organic analysis 2. State of the Art. 1990. American Laboratory 22 (12), 28.

Potthoff, M., Joergensen, R.G., Wolters, V., 2001. Short-term effects of earthworm activity and straw amendment on the microbial C and N turnover in a remoistened arable soil after summer drought. Soil Biology & Biochemistry 33, 583–591.

Pulleman, M., Tietema, A., 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. Soil Biology & Biochemistry 31, 275–285.

Schjønning, P., Thomsen, I.K., Moldrup, P., Christensen, B.T., 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. Soil Science Society of America Journal 67, 156–165.

Six, J., Elliott, E.T., Paustian, K., Doran, J.W., 1998. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. Soil Science Society of America Journal 62, 1367–11377.

Sparling, G.P., Ross, D.J., 1988. Microbial contributions to the increased nitrogen mineralization after air-drying of soils. Plant and Soil 105, 163–167.

Stark, J.M., Smart, D.R., Hart, S.C., Haubensak, K.A., 2000. Regulation of nitric oxide emissions from forest and rangeland soils of western North America. Ecology 83, 2278–2292.

Steenwerth, K.L., Jackson, L.E., Calderón, F.J., Stromberg, M.R., Scow, K.M., 2003. Soil microbial community composition and land use history in cultivated and grassland ecosystems in coastal California. Soil Biology & Biochemistry 35, 489–500.

Swift, M.J., van der Meer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C.K., Hawkins, B.A., 1996. Biodiversity and agroecosystem

function. In: Mooney, H.A., Hall Cushman, J., Medina, E., Sala, O.E., Schulze, E.D. (Eds.), Functional Roles of Biodiversity: a Global Perspective. John Wiley and Sons, Chichester, pp. 261–298.

Tunlid, A., White, D.C., 1992. Biochemical analysis of biomass community structure, nutritional status and metabolic activity of microbial communities in soil. In: Stotzky, G., Bollag, J.M. (Eds.), Soils, Plants, and the Environment. Soil Biochemistry, vol. 7. Marcel Dekker, New York, pp. 229–262.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology & Biochemistry 19, 703–707.

van Gestel, M., Ladd, J.N., Amato, M., 1992. Microbial biomass responses to seasonal change and imposed drying regimes at increasing depths of undisturbed topsoil profiles. Soil Biology & Biochemistry 24, 103–111.

van Gestel, M., Merckx, R., Vlassak, K., 1993a. Microbial biomass responses to soil drying and rewetting: the fate and fast- and slow-growing microorganisms in soils from different climates. Soil Biology & Biochemistry 25, 109–123.

van Gestel, M., Merckx, R., Vlassak, K., 1993b. Soil drying and rewetting and the turnover of ^{14}C-labelled plant residues: first order decay rates of biomass and non-biomass ^{14}C. Soil Biology & Biochemistry 25, 109–123.

Venterea, R.T., Rolston, D.E., 2000. Mechanisms and kinetics of nitric and nitrous oxide production during nitrification in agricultural soil. Global Change Biology. 6, 303–316.

Vestal, R., White, D., 1989. Lipid analysis in microbial ecology. Bioscience 39, 535–541.

Waring, S.A., Bremner, J.M., 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability in forest soils. Nature 201, 951–952.

Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation–extraction—an automated procedure. Soil Biology & Biochemistry 22, 1167–1169.

Zelles, L., Bai, Q.Y., Rackwitz, R., Chadwick, D., Beese, F., 1995. Determination of phospholipid- and lipopolysaccharide-derived fatty acids as an estimate of microbial biomass and community compositions in soils. Biology and Fertility of Soils 19, 115–123.